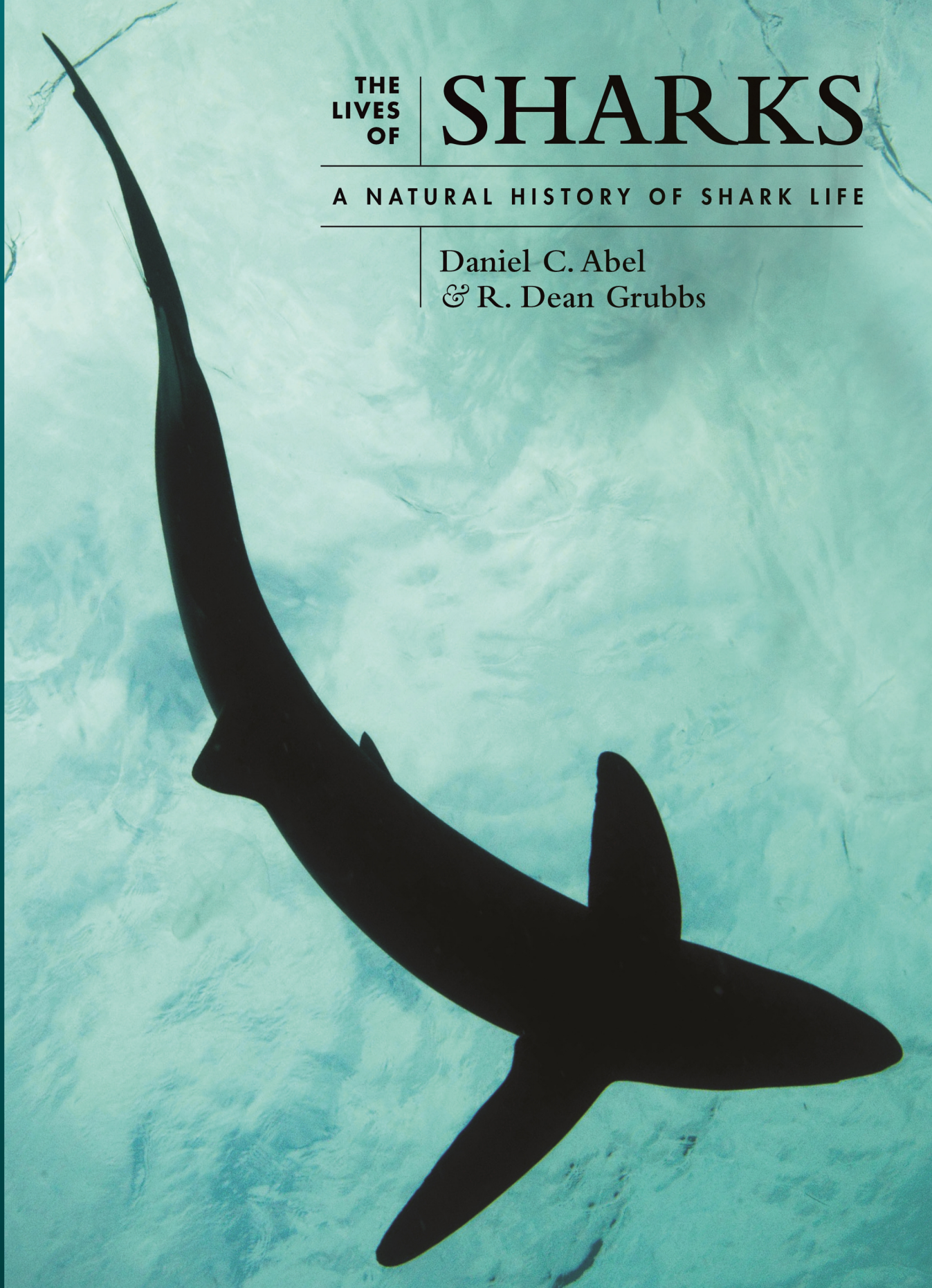

THE LIVES OF SHARKS

A NATURAL HISTORY OF SHARK LIFE

Daniel C. Abel
& R. Dean Grubbs

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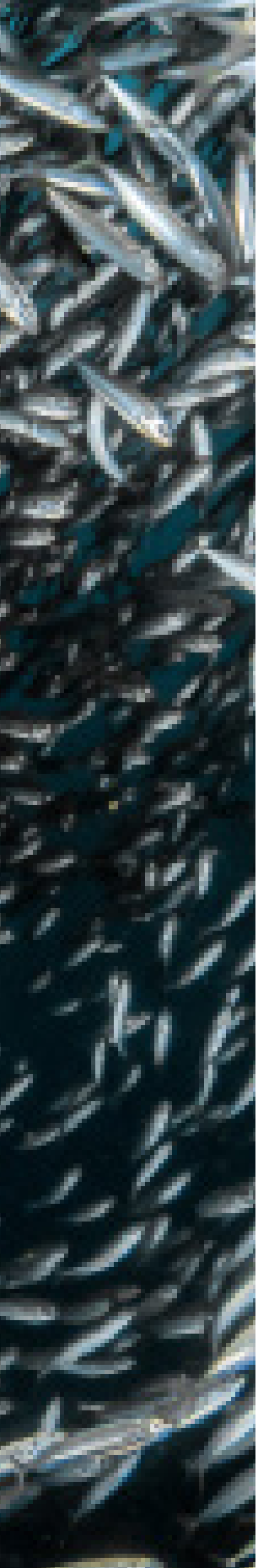

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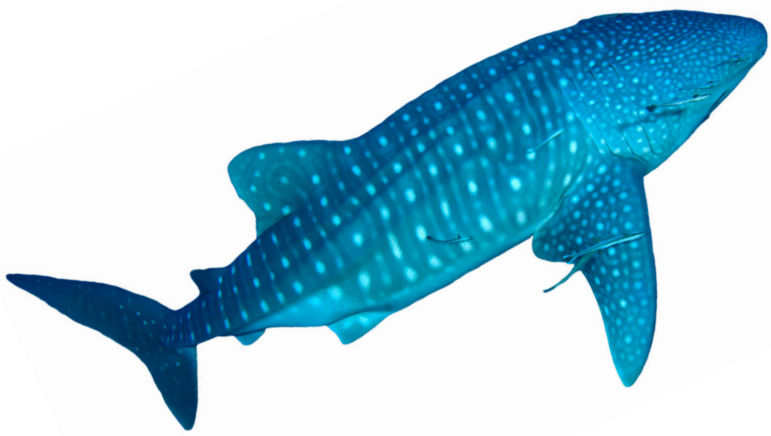

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INTRODUCTION

The world of sharks

Every May for nearly 30 years we have taught a course in shark biology at the Bimini Biological Field Station in The Bahamas. Within hours of our arrival in this tropical paradise, we repeat a ritual that culminates in what our students have been waiting their entire lives to experience: snorkeling with wild, actively feeding, 8 ft (2.5 m) Caribbean Reef Sharks (*Carcharhinus perezi*; page 234).

When you close your eyes and envision a shark, the chances are it looks like a Caribbean Reef Shark: a graceful, magnificent, sleek, heavily muscled gray predator. These are the beasts of your dreams if you're a shark lover, or perhaps your nightmares if you aren't. Surprisingly, the students are silent in the skiffs as they await our short boat ride, and the air is tinged with a palpable dose of nervous anticipation mixed with a sense of impending terror. You can almost read some of their minds as they question the wisdom of enrolling in the course. *What have we gotten ourselves into?*

We motor 15 minutes over almost brazenly azure seas to our destination, a stony outcrop known as Triangle Rocks. Within minutes, as the students prepare to slip into the crystal-clear water, large Caribbean Reef Sharks appear one by one and execute a series of ever-tightening circles around our boats, drawn from perhaps a mile or more away by the sound of our outboard motors. This sound informs them that the aquatic equivalent of a buffet might soon commence, and who in their right mind passes up free food? The sharks have done this before, so they know the drill: wait until the students are aligned shoulder to shoulder, grasping a floating rope stretching from the stern of the biggest boat, then the feeding will start, as chunks of fish are tossed into the water. While the sharks may know what awaits, the students do not, since this is a novel experience for them. It's one thing to watch divers observing sharks from the safety of a metal cage on TV, but it's a totally foreign experience to be immersed into a mob of 8 ft sharks that suddenly look much, much larger than the students envisioned.

What brought the students and us to this point is an unabashed fascination with, and love of, sharks—animals we have been conditioned our entire lives to fear. But we, our students, and you, we suspect, rise above that fear. Instead, we marvel at the prowess of sharks as predators and their undeniable grace, even as they devour their unlucky prey. We are mesmerized by their presence, whether on TV, in an aquarium, or especially, in nature. We want to know more about them. What did sharks look like early in their evolutionary history? How many kinds of sharks are there and how do they differ from one another? Do sharks live in rivers and lakes? What makes them such effective predators? Are we justified in fearing them? How stable are shark populations and what threatens them? What would the oceans be like without sharks? What can we do to make sure that doesn't happen?

→ Caribbean Reef Sharks (*Carcharhinus perezi*) silhouetted against downwelling light under a dive boat in the clear tropical waters of The Bahamas.

Surprisingly, within minutes of arriving at Triangle Rocks, almost all the students are in position to watch what the public might call a feeding frenzy but which is more aptly described as "the dance of the sharks." Some students jockey to be the first to leave the perceived safety of the boat to swim with the sharks, the number of which by that point has grown to perhaps a dozen. Others are more hesitant, but all eventually transition into the briny sea and take their place shoulder to shoulder on the floating rope. The scene has now transitioned from so-called "shark-infested waters" to what might more appropriately be labeled as "human-infested."

It took 450 million years of evolution to perfect the form, senses, and behavior of these sharks, but it is a mistake to consider them primitive, since other vertebrates—specifically the bony fishes (for example, cod, tuna, and bass) and reptiles—trace their early evolution to the same geological era as sharks. The Caribbean Reef Shark does not look remotely like its early ancestors, although it does possess many of the same characteristics that define it as a shark (pages 22–27). Over their relatively long evolutionary history, the majority of these ancient relatives became extinct, leaving behind what we know as modern sharks. But the Caribbean Reef Shark has one major characteristic in common with both its ancestors and other modern sharks: it is a predator.

When the first chunk of bait hits the water, the dance begins. No movement is wasted or haphazard. The sharks' senses allow them to hear the splash of the bait and to determine its location. The bait's rapidly spreading odor provides more clues to its location, and draws in even more sharks as it spreads into the surrounding area. Watching the last part of the sharks' approach to the chunk of fish that was tossed into the water only seconds earlier is the most fascinating aspect of this spectacle. As one or more sharks move into position to be the first to gobble the bait, their vision

↖ A solo Caribbean Reef Shark cruising the shallow waters of The Bahamas. This species is the most common shark of Caribbean coral reefs and it occupies a similar ecological niche to the Indo-Pacific Grey Reef Shark (*Carcharhinus amblyrhynchos*).

↑ Lemon Sharks (*Negaprion brevirostris*), distinguished by their muted yellowish tint and two similarly sized dorsal fins, are found in the shallows of temperate and tropical Atlantic and eastern tropical Pacific coasts.

↓ A diver feeding a Great Hammerhead (*Sphyrna mokarran*) in Bimini, The Bahamas, while Nurse Sharks (*Ginglymostoma cirratum*) and a variety of bony fishes scavenge for the scraps.

in this clear water allows them to move swiftly directly toward it, aided by their powerful swimming musculature and ability to fine-tune their movement using their complement of fins. Since their prey in natural circumstances might fight back, the sharks are programmed to close their eyes as they open their mouths about 3 ft (1 m) or so from the bait. If the bait were a live fish, the sharks would detect the minute electrical currents that all living organisms emit, and this signal would guide them to the prey with surgical precision, which was first demonstrated in cat sharks.

After an hour or so of observing the shark ballet, the students are hooked for life. The conversations we overhear the rest of the day reflect the passion that shark lovers all over the world share. Their nervous jitters have been replaced with goose bumps as they reflect on the experience, which most call the greatest of their lives. And it is only the first day of the course! Over the next six days, they will swim with, observe, or

otherwise study Tiger Sharks (*Galeocerdo cuvier*; page 232), Nurse Sharks (*Ginglymostoma cirratum*; page 40), and other species.

Students in the shark biology class will also learn the same basic content we have included in *The Lives of Sharks*. This book delves into sharks in all of their multidimensional facets, from the roles they play in our lives, to how human activities threaten theirs. We discuss how sharks have changed and how they have stayed the same over the course of their 450 million-year evolutionary history. We cover the diversity of shapes, sizes, lifestyles, habitats, and ecological roles of the 500-plus species living today, challenging what you think of as a typical shark. Throughout the book we reflect on the suite of adaptations that make sharks such effective predators and that have allowed them to occupy almost all divisions of the ocean and even some freshwater habitats. We consider the unimaginable situation of what the world's oceans would be like without sharks.

The sharks we have chosen represent a broad cross section of iconic species that we are certain you know, including the White Shark (*Carcharodon carcharias*; page 106) and Whale Shark (*Rhincodon typus*; page 144). But we also include an array of species most readers might not be as familiar with, such as the Goblin Shark (*Mitsukurina owstoni*; page 166) and Swell Shark (*Cephaloscyllium ventriosum*; page 42). And we include one of the most endangered fish in the sea, the Smalltooth Sawfish (*Pristis pectinata*; page 112), which is actually a ray, a shark relative whose body shape and position in the food chain belie the fact that it is not a shark. Not all of our profiled species are apex predators, since most species of shark are not at the very top of the food chain.

Our journey into the lives of sharks is a celebration of these magnificent and endlessly fascinating creatures, but it is also an examination of their biology, ecology, behavior, and conservation. While this book cannot repeat the experience of swimming with sharks, we hope that our love of sharks and our passion for shark conservation shine sufficiently in this book to satisfy your own love of these sometimes misunderstood, infinitely interesting, mysterious predators.

Daniel C. Abel and R. Dean Grubbs

Shark classification

Currently, 36 families and about 543 species of sharks are known to science. Rightfully, since they are all chondrichthyans, we should add the batoids and chimaeras to this list, bringing the total to 61 families and about 1,300 species. Using the classic taxonomic hierarchy of life, all chondrichthyans are in the domain Eukarya, kingdom Animalia, phylum Chordata, subphylum Vertebrata (or Craniata), and superclass Gnathostomata.

Your dog, cat, pet fish, and you yourself are in these same categories. So are all of the bony fishes (minus the relatively few jawless forms), amphibians, reptiles, birds (or avian reptiles), and mammals. Sharks, batoids, and chimaeras are all members of the class Chondrichthyes. Within the Chondrichthyes are two subclasses: Holocephali (chimaeras, or ghost sharks) and Elasmobranchii, the most species-rich and diverse chondrichthyans. Elasmobranchs are further subdivided into three superorders: Batoidea (skates and rays), Squalomorphii (about 179 extant, mostly cold-water, species), and Galeomorphii (about 364 species representing a diverse array of sharks).

A LIST OF SHARK FAMILIES

The 36 taxonomic families of sharks that are currently recognized, along with their common names and the number of species. There are 11 and 25 families in the superorders Squalomorphii and Galeomorphii, respectively.

SUPERORDER

SQUALOMORPHII (DOGFISH SHARKS)

Chlamydoselachidae
Frilled sharks (Two species)

Hexanchidae →
Cow sharks (Five species)

Echinorhinidae
Bramble or prickly sharks
(Two species)

Squatinidae
Angel sharks (22 species)

Pristiophoridae
Sawsharks (10 species)

Squalidae
Dogfish sharks (39 species)

Centrophoridae
Gulper sharks (16 species)

Etmopteridae
Lantern sharks (51 species)

Somniosidae
Sleeper sharks (17 species)

Oxynotidae
Rough sharks (Five species)

Dalatiidae
Kitefin sharks (10 species)

SUPERORDER

GALEOMORPHII (GALEOMORPH SHARKS)

Heterodontidae
Bullhead or horn sharks
(Nine species)

Parascylliidae
Collared carpet sharks
(Eight species)

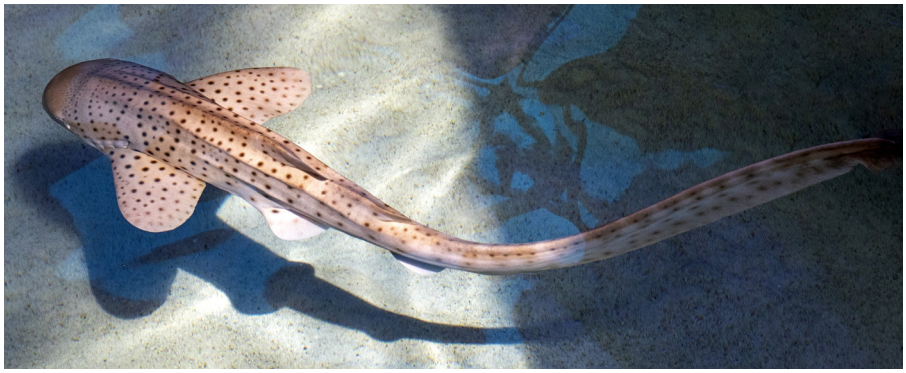
Brachaeluridae
Blind sharks (Two species)

Orectolobidae
Wobbegongs (12 species)

Hemiscylliidae ↑
Bamboo or longtailed
sharks (17 species)

Ginglymostomatidae
Nurse sharks (Four species)

Stegostomatidae ↓
Zebra Shark (One species)



Rhincodontidae ↑
Whale Shark (One species)

Odontaspididae
Sand tigers (Three species)

Pseudocarchariidae
Crocodile Shark (One species)

Mitsukurinidae
Goblin Shark (One species)

Megachasmidae
Megamouth Shark (One species)

Alopiidae
Thresher sharks (Three species)

Cetorhinidae
Basking Shark (One species)

Lamnidae
Mackerel sharks (Five species)

Scyliorhinidae →
Cat sharks (49 species)

Proscylliidae
Finback cat sharks
(Seven species)

Pseudotriakidae
False cat sharks (Six species)

Leptochariidae
Barbeled Houndshark
(One species)

Pentanchidae
Deep-sea cat sharks
(110 species)

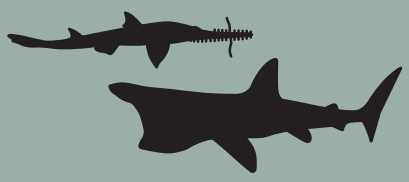
Triakidae
Houndsharks (47 species)

Hemigaleidae
Weasel sharks
(Eight species)

Carcharhinidae
Requiem sharks
(57 species)

Galeocerdidae
Tiger Shark (One species)

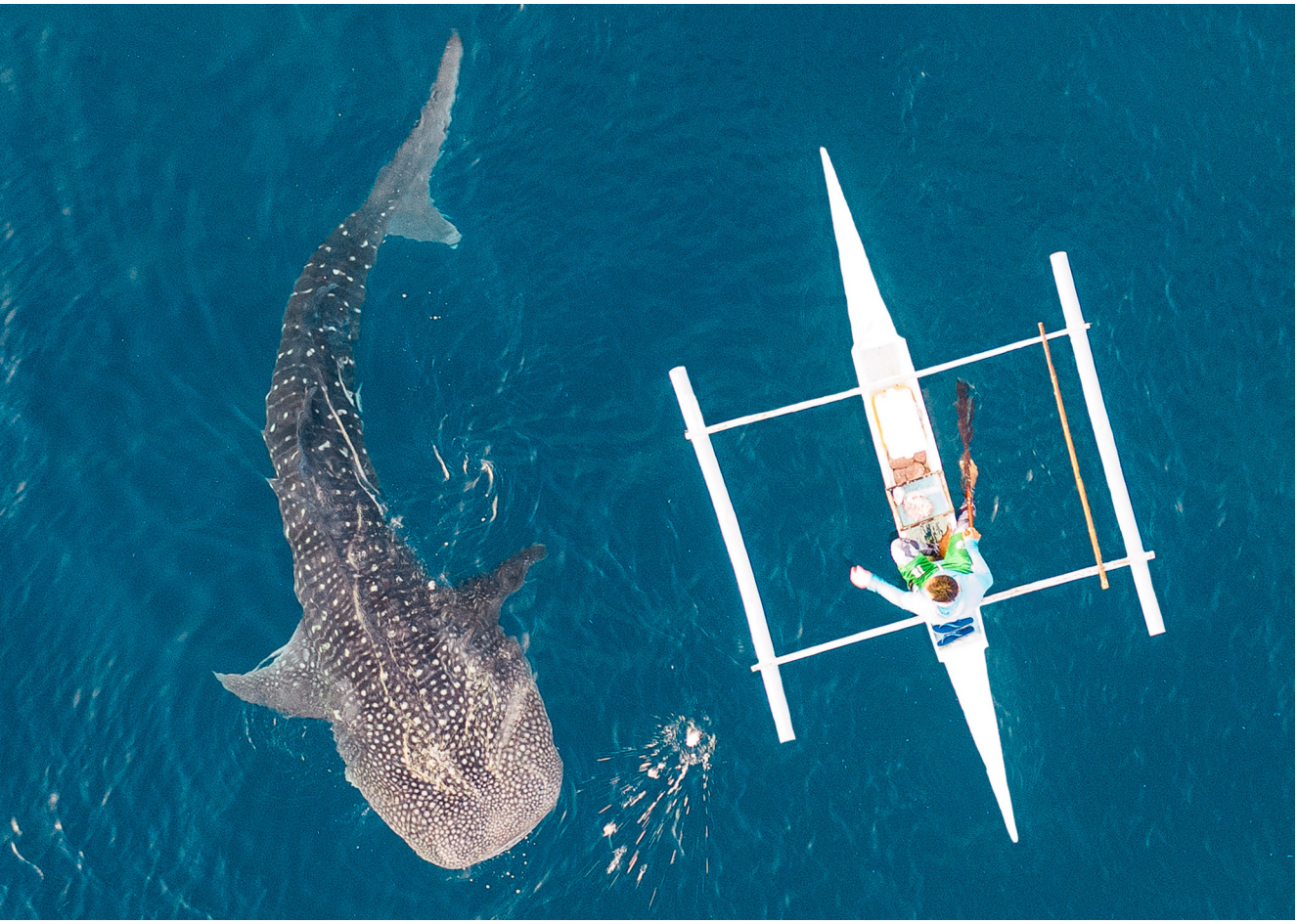
Sphyrnidae →
Hammerhead sharks
(Nine species)



THE EVOLUTION & DIVERSITY OF SHARKS

Sharks in our lives

Our lives intersect with sharks in many ways, as objects of our admiration, fascination, recreation, respect, scholarly study, economy, and unfortunately, as paragons of fear. It would be disingenuous to ignore the last of these, since the primal dread that many harbor for this group of predators overwhelms the positive feelings of others. But any fear we feel should be placed firmly in perspective.



→ The Blacktip Shark (*Carcharhinus limbatus*), a swift-swimming consumer of small schooling fishes, is imputed to be the source of infrequent bite-and-release interactions with swimmers along the southeast US coast.

↙ A drone view of a Whale Shark (*Rhincodon typus*), the largest extant fish, in the Phillippines. Gatherings of these large plankton-eating beasts here and in other areas have led to massive influxes of tourists, often to the detriment of the sharks.

As we acknowledge that sharks occasionally bite and, sadly, even kill people, let us equally recognize that these events are extremely rare. Should you be afraid of swimming at the beach? Of course! But not because of sharks. More immediate dangers include being struck in the head by a Jet Ski or surfboard, being exposed to toxic pollutants or unhealthy bacteria, or being sucked into the surf by an undertow or whisked offshore by rip currents.

Both of the authors have been bitten by sharks—numerous times in fact—as have most other shark scientists. In virtually all cases, these bites occur as we handle a shark by removing it from its habitat as part of our research. Consider this: divers, swimmers, and scientists spend countless hours in shark habitat, knowingly or not, with very few negative interactions. But shark bites (called "bites" because they are considered relatively minor, mistaken-identity events) and shark attacks (which imply defensive behavior or involve more serious, repeated contacts) do happen.

The reality is that sharks are far more important to us than as mere objects of our fear. Sharks that are top-level predators stabilize ecosystems, and shark ecotourism bolsters local economies and is a driving force for conservation of marine ecosystems. Sharks are useful in a number of biomedical applications (for example, shark-liver oil is an ingredient in a widely used antihemorrhoidal cream and antibacterial coatings), and they are fished for meat and fins, in some cases sustainably. But paramount to those of us who can transcend the fear factor, sharks captivate us by their beauty, grace, behaviors, and adaptations.

RARE OCCURRENCES

According to the International Shark Attack File, an authoritative database of both shark bites and attacks, in 2021 there were only 79 unprovoked human–shark interactions and 39 provoked bites. These are certainly underestimates, since interactions occurring in more remote or sparsely populated areas are very likely underreported, but even so the true total will still be low.

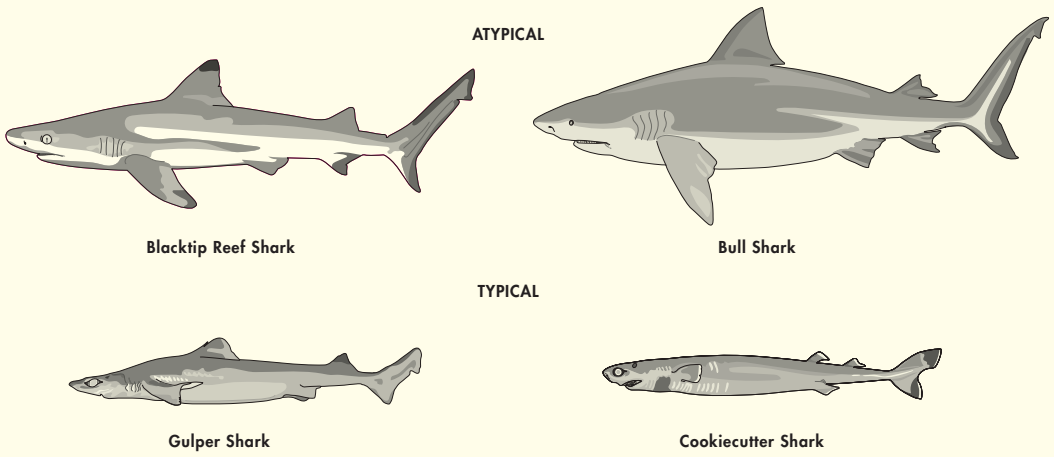
What is a shark?

Unless you are thinking of a Gulper Shark (*Centrophorus granulosus*) or Swell Shark (*Cephaloscyllium ventriosum*; page 42), when you envision a shark you are likely thinking of a streamlined, large (more than 3 ft/1 m) gray shark that lives along shorelines, such as a Blacktip Reef Shark (*Carcharhinus melanopterus*) or Great White Shark (*Carcharodon carcharias*; page 106), which is referred to from now on by its accepted common name, White Shark. The iconic species you conjure up seem representative of sharks as a group, since these are the species we interact with, mostly through the media but in many cases when we dive with them. However, these are, in fact, the oddballs.

To see a typical shark you must either visit the deep sea (defined as ocean deeper than 650 ft/200 m), or be a deep-sea commercial fisher or shark biologist. That is because about two-thirds of the 543 known species of living sharks are 3 ft (1 m) or smaller in length and more than half of them live in the deep sea. Perhaps to the dismay of those who watch sensationalized shark documentaries on TV, a typical shark is small and brown, and lives in the deep ocean.

The new normal

You might consider large coastal sharks like the Blacktip Reef Shark (*Carcharhinus melanopterus*) or Bull Shark (*Carcharhinus leucas*) as typical, but small, deep-sea sharks, such as the Gulper and Cookiecutter Sharks (*Isistius brasiliensis*), are in fact more representative.

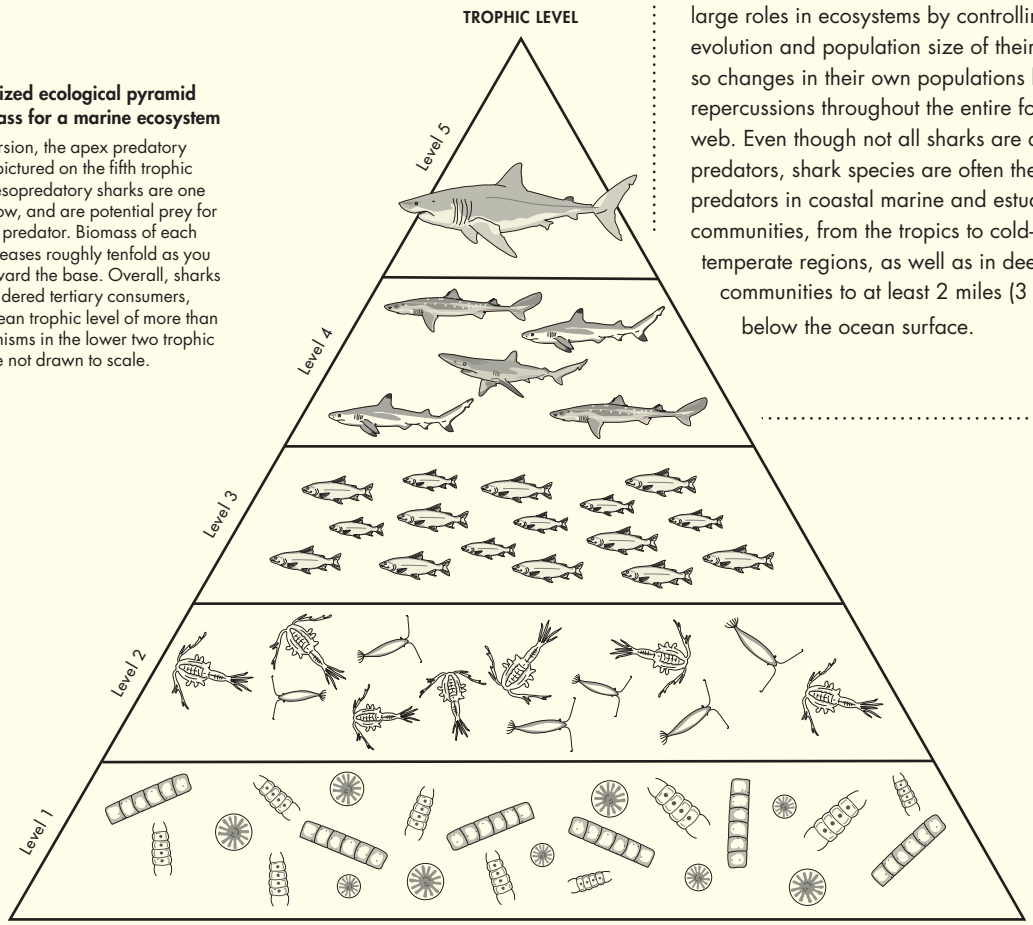


The environmental conditions of the deep sea are very different from those of shallow ecosystems, to the extent that only a handful of sharks are able to live in or travel between both. Living in the cold, dark, food-poor deep-sea environment means evolving adaptations to conserve energy, locate prey, avoid being prey yourself, and find mates. And these adaptations are the sources of departures from the fast-swimming, large-bodied gray forms of most coastal sharks. However, there is one way in which deep-sea sharks are typical: in several cases their populations are threatened by human impacts.

TOP PREDATORS

Contrary to popular belief, not all sharks are apex predators—that is, they are not at the top of the food chain. However, all sharks—even plankton-eating species such as Whale and Basking Sharks (*Rhincodon typus* and *Cetorhinus maximus*, respectively)—are predators. Most shark species, including the Port Jackson Shark (*Heterodontus portusjacksoni*) and Nurse Shark (*Ginglymostoma cirratum*), plus all of the dogfish sharks and smooth-hound sharks, would be considered mesopredators, one or more levels below the top shark predators, which include the White Shark, Bull Shark (*Carcharhinus leucas*), and Oceanic Whitetip Shark (*C. longimanus*).

Predators often play disproportionately large roles in ecosystems by controlling the evolution and population size of their prey, so changes in their own populations have repercussions throughout the entire food web. Even though not all sharks are apex predators, shark species are often the top predators in coastal marine and estuarine communities, from the tropics to cold-temperate regions, as well as in deep-sea communities to at least 2 miles (3 km) below the ocean surface.



Generalized ecological pyramid of biomass for a marine ecosystem

In this version, the apex predatory shark is pictured on the fifth trophic level. Mesopredatory sharks are one level below, and are potential prey for the apex predator. Biomass of each level increases roughly tenfold as you move toward the base. Overall, sharks are considered tertiary consumers, with a mean trophic level of more than 4. Organisms in the lower two trophic levels are not drawn to scale.

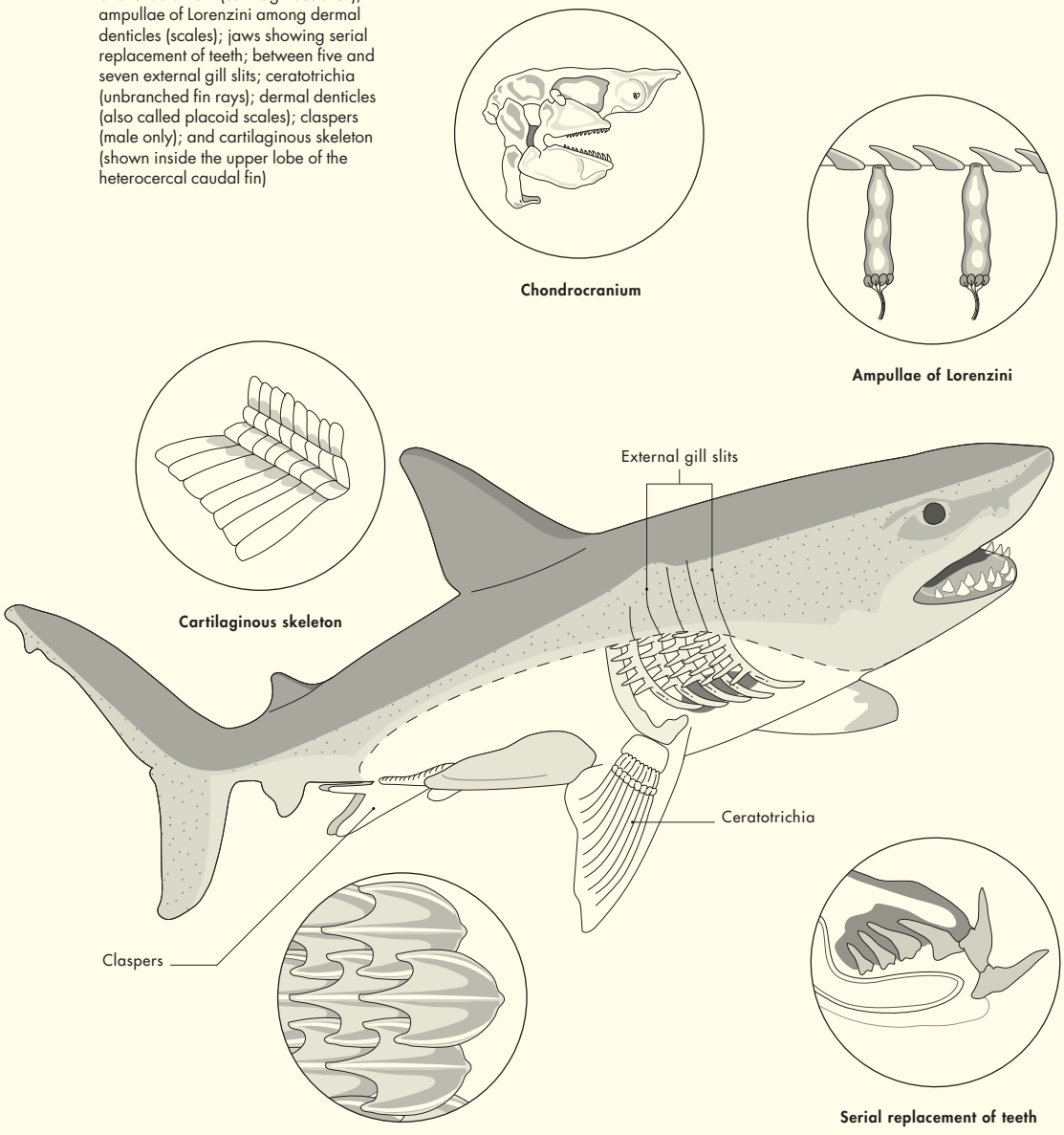
DISTINGUISHING FEATURES

Sharks, along with their close relatives the batoids (rays and skates) and chimaeras (ghost sharks), belong in the taxonomic class Chondrichthyes, which translates to "cartilaginous fishes," a reference to the principal material comprising their skeleton. Among the nearly 74,000 species of living vertebrates, bone wins outright as the main structural component, making up the skeletons of the bony fishes (around 35,000 species), amphibians (8,400 species), non-avian reptiles (11,700 species), birds (or, more correctly, avian reptiles; 11,200 species), and mammals (6,600 species). Cartilage also forms the skeletal framework of a few "bony" fishes (coelacanths, sturgeon, paddlefish, and bichirs) but is the exclusive component in the 1,245 species of chondrichthyans, a group that breaks down into about 543 species of sharks, 651 batoids, and 53 chimaeras. These numbers increase as scientists discover new species. For example, 40 years ago there were only 342 known species of shark.

In addition to possessing cartilage, sharks have a number of other characteristics that distinguish them from bony fishes. For one, they have 5–6 external gills slits on either side of the head. In batoids, which evolutionarily split from sharks more than 250 million years ago, the 5–7 gill slits are present, but on the underside of the body. Bony fishes have a single bony operculum covering their gills. Another external distinguishing feature is the heterocercal caudal (tail) fin of sharks, in which the upper lobe is longer than the lower lobe. Both lobes of the caudal fin of bony fishes are characteristically equal in length.

Distinguishing characteristics of sharks

Clockwise from top: Simple one-piece chondrocranium (cartilaginous skull); ampullae of Lorenzini among dermal denticles (scales); jaws showing serial replacement of teeth; between five and seven external gill slits; ceratotrichia (unbranched fin rays); dermal denticles (also called placoid scales); claspers (male only); and cartilaginous skeleton (shown inside the upper lobe of the heterocercal caudal fin)



← The head of a juvenile Scalloped Hammerhead (*Sphyrna lewini*) in Kane'ohe Bay, Hawai'i (left). Underlying the oddly-shaped head is a laterally expanded cartilage, the material that comprises the skeleton of all sharks. The caudal fin of a Whale Shark (right). This asymmetrical fin, with its elongated upper lobe, which is stabilized by internal vertebral elements, is characteristic of sharks as a group.

The reproductive lives of sharks are another distinguishing feature, as well as being incredibly fascinating. Sharks differ from the overwhelming majority of bony fishes in that they use a method of transferring sperm to the female that is more often associated with terrestrial vertebrates and marine mammals, namely internal fertilization. Male sharks have two claspers—modifications of the inner margin of the pelvic fins—one of which is inserted into the female. This serves as both an anchoring device and conduit for a brew of seawater and semen, which is flushed into the female's reproductive tract.

Additional shark characteristics include tooth-like placoid scales, a protective eyelid (called the nictitating membrane) in some species, an oil-filled liver (which provides additional buoyancy), a spiral-valve intestine (an unusual adaptation for increasing surface area for food absorption), ampullae of Lorenzini (pores on the head that detect extremely minute electrical fields), and soft fin rays (known as ceratotrichia). This last feature has contributed to the demise of numerous species, since the ceratotrichia, when dried and processed, are the essential ingredient in the Asian delicacy shark fin soup, for which demand is still high despite global campaigns to discourage consumption.

↑ The head of a Sand Tiger (*Carcharias taurus*) displaying multiple rows of teeth and ampullae of Lorenzini, electrosensory pores on its snout.

↖ Mating in Whitespotted Bamboo Sharks (*Chiloscyllium plagiosum*), one of a small number of shark species in which mating has been observed (left). One of the claspers of the male—on the right—is shown inserted into the cloaca of the female. Partially-closed nictitating membrane of a Blue Shark (*Prionace glauca*; page 138 – right). This scale-covered protective structure is found in requiem sharks, and similar structures occur in some birds, lizards, frogs, and even a few mammals (such as seals, polar bears, camels, and aardvarks).

NO TEETHING TROUBLES

If you are a collector of shark teeth, one distinguishing shark characteristic feeds your hobby: serial tooth replacement, or the presence of multiple rows of teeth in various stages of development. Shark teeth are not deeply embedded in the jaw cartilage, but rather move on a looser "conveyor belt" of connective tissue. This constitutes yet another way in which sharks have moved in a different evolutionary direction than all other vertebrate predators. When a terrestrial vertebrate predator such as a Leopard (*Panthera pardus*) loses one of its canine teeth, which are deeply rooted in bone, it enters a dangerous state of competitive disadvantage, since starvation is a major cause of mortality among terrestrial and many marine top predators. Sharks, on the other hand, have planned in advance, evolutionarily speaking, for the certainty of tooth loss. When a tooth becomes dislodged (such as after hitting a bone in a prey animal), it, along with the rest of the entire outer row, is replaced when a new row of sharpened, unworn teeth moves into place. A shark may shed a row of teeth every few weeks or so and go through thousands of teeth over its lifetime.

Why are there more kinds of catfish than sharks?

There are 36 families and 543 species of shark alive today, which may seem an impressive number until you consider that there are more than 435 families and 35,000 species of bony fishes. Even when the other members of the class Chondrichthyes, the batoids and chimaeras, are included, the number of species rises to only around 1,300, or 1.7 percent of known living vertebrates. In comparison, at nearly 4,000 species the taxonomic diversity of catfishes, just one group of bony fishes, is about triple the number of sharks, batoids, and chimaeras combined.

REPRODUCTION STRATEGIES

New species often form following some circumstance or event that separates a population of an existing species. A number of explanations exist for the relatively low speciation rate, and hence low diversity, of sharks and their relatives compared to the bony fishes.

For a start, bony fishes have more offspring than sharks—in other words, they are more fecund. Most bony fishes have external fertilization and invest a small amount of resources into a large number of eggs (several million in the case of pollack, for example).

← The egg cases of a cat shark with early embryos developing within. Egg-laying occurs only in small species of sharks; after a few weeks of development, seams in the egg case dissolve, allowing seawater to enter and the gradually toxifying contents to leave.

→ A rare photo of the birth of a Lemon Shark (*Negaprion brevirostris*) in Bimini, Bahamas. Note the umbilical cord still partially attached to the neonate shark and its mother.